INSELBERGS: VEGETATION, DIVERSITY AND ECOLOGY

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Summary

Inselbergs are rock outcrops which rise more or less abruptly above a plain. They can be met all over the world in tropical and subtropical climates. Because of their

geomorphologic delimitation from the surroundings and because of their isolation, inselbergs represent independent ecosystems which are especially suitable for comparative research on structure and dynamics of plant biodiversity and for studying mechanisms of ecophysiological adaptation in plants. The following treatise describes the geomorphologic genesis and physiognomy of inselbergs. It characterizes the diverse inselberg sub-habitats and the physiognomy of the vegetation linked to them, and the "strategies" developed by inselberg plants to sustain the ecophysiological stress created by their specific environment. Finally the relations of humans to inselbergs will be considered briefly.

1. Introduction

Inselbergs (d`emprunt from German *Insel* = island and *Berg* = mountain) represent characteristic rock outcrops which rise suddenly above a plain, hilly country or rain forests. They always form distinguished landscape elements isolated from each other like islands in an ocean. The term "Inselberg" is just a metapher to illustrate their ecolological isolation. In fact, except of isolation there are no ecological similarities between the Inselbergs on the land surface and the island in the oceans. Inselbergs can be met all over the world in tropical and subtropical climates, or where a tropical climate dominated during the history of earth. Because of their exposed position in the landscape, since thousands of years inselbergs stimulated the fantasy of humans so that many of them gained important spiritual meaning and became sacred centers for the indigenous populations. Moreover, inselbergs are far-off visible landmarks and meeting points for the nomads.

Recently inselbergs attracted strong attention also by scientists, particularly by botanists and ecologists. Although noticed and described by Alexander von Humboldt already in 1819 (after his journey along the Orinoco River), the awareness of the great versatility of inselbergs for comparative botanical and ecological research has emerged only since the 1980s. Until now, some hundred inselbergs in Africa, Madagascar, Australia and South America have been investigated.

The great scientific interest in inselbergs derives from several reasons. First, inselbergs belong to the nowadays extremely rare unspoiled and therefore particularly precious ecosystems. In order to develop effective strategies to protect the inselberg ecosystems it is required to learn more about the composition of inselberg life communities, their changes in response to variations in the constellation of biotic and abiotic factors at their specific environment, and their sensitivity towards anthropogenic influences. Second, aiming to understand functioning of ecological networks it is reasonable to focus research on this topic on such ecosystems and groups of organisms where, because of lower complexity, it is easier to overlook ecological coherences. Inselbergs fit this demand in an ideal manner. Third, studies on inselberg ecosystems are suitable to answer some basic ecological questions, for instance regarding the minimum size of species populations required to guarantee their survival at a given habitat and the consequences of fragmentation of populations for their stability. Inselbergs represent also centers of biodiversity thus providing suitable model systems to investigate its structure and dynamics. Finally, living conditions on inselbergs are particularly demanding to the organisms occupying this special habitat. For this reason, inselbergs are very suitable sites for comparative studies on mechanisms and effectiveness of ecological adaptation in organisms.

In the following we shall consider the genesis and physiognomy of inselbergs, analyze the climatic and edaphic conditions and relate them to the structure and dynamics of the inselberg vegetation. Research on the fauna of inselbergs is still at its beginning and thus will remain beyond the scope of the present chapter.

2. Geomorphologic Genesis and Physiognomy

It has been already mentioned that inselbergs represent characteristic rock outcrops (Figure.1A, B). Because of the geomorphologic delimitation from their surroundings and because of their isolation they represent independent ecosystems with specific microclimatic and edaphic conditions and correspondingly adapted biocoenoses.

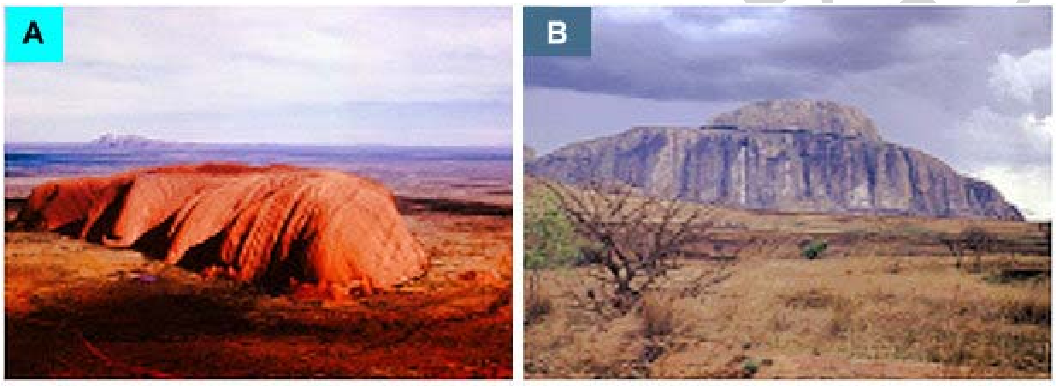

Figure 1A . The Uluru (Ayers Rock), an arcose inselberg in the center of Australia; in the background the Kata Tjuta (Mt. Olgas); B:Granitic Inselberg near Zazafotzy (Central Plateau of Madagascar)

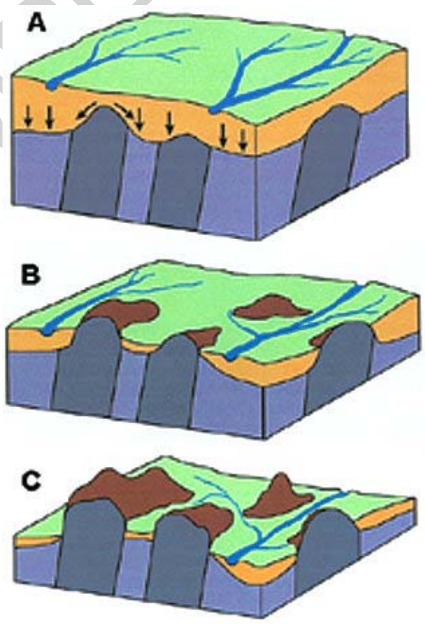

Figure 2. The genesis of inselbergs. The initial state of inselberg evolution is a plain where moisture (arrows) penetrates the soil covering rock formations (A). At the boundary between soil and rock the water accumulates and intensifies there a deep weathering of the rock. Differences in the rock compactness create unevenness in the weathering front thus initiating the sculpturing of the rock outcrops called inselbergs. The eroded material is transported away by the drainage ditches so that the tips of the rock inequalities begin to break through the declining soil cover (B). By further erosion and transport the final state of inselberg evolution is reached (C)

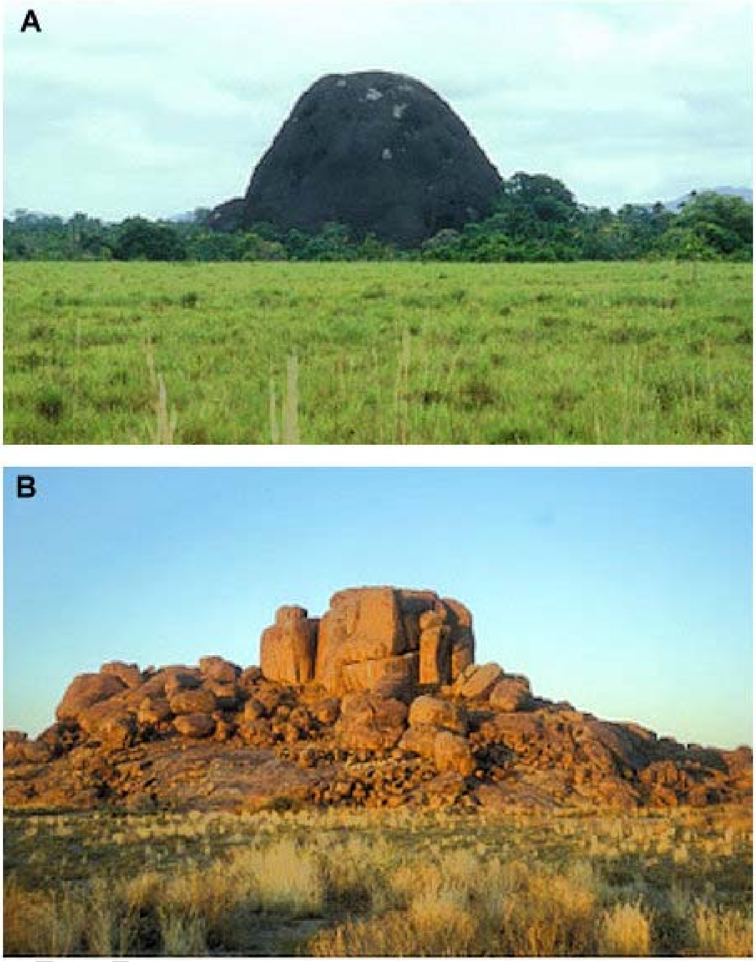

Figure 3 A. Dome inselberg (“bornhardt) at the Orinoco River, Venezuela; B: Castle kopje, southern Namibia.

Inselbergs consist of monolithic blocks of hard, geologically very old material dating back on the average 50 x 10^6 years, mostly granite or gneiss, exceptionally sandstone. As shown in Figure.2, inselbergs are the product of deep and under tropical conditions especially intensive weathering. Their altitude ranges from few to several hundreds of meters and their extension can reach several km^2.

According to genesis and morphology, several types of inselbergs are distinguished. When hard rock formations become uncovered by the process of double planation, they first form flat shield inselbergs. As erosion processes carry on in the surrounding area, exposing the inselbergs more and more over time, they might develop into morphologically different forms like whale backs (Figure. 1B), domes ("Glockenberg", "bornhardt"; Figure. 3A), castle kopjes (Figure. 3B), or table mountains (mesa).

Inselbergs are not only morphologically well distinguished from their surrounding but also by the climatic parameters. On a first view, living conditions for organisms on inselbergs appear extraordinarily hostile, since bare rock surfaces are dominating. Occasionally they are covered by heaps of small rocks and rock debris. Quick water drainage limits availability of water even in the wet season. In the rainless season most sites on inselbergs are extremely dry and hot. During midday the rock surface may easily heat up to temperatures in the range of 65 ^{o}C, and during the dry season precipitation can be interrupted for weeks or even months.

However, a closer look shows that inselbergs by no means represent uniformly hostile systems. They rather exhibit clear fragmentation in sub-habitats providing various ecological niches which largely differ in the constellation of edaphic and microclimatic factors. For instance, some areas of the rock may be covered by sparse soil layers. There are clefts and gaps between rocks and depressions on top or on the slopes of the rocks where humus can accumulate. Such gaps often provide permanent shade together with high soil and air humidity. A few meters away the open rock surface is exposed to full sun radiation, and thus, is extremely dry. In contrast, even wet flushes, seasonal and even permanent rock pools may occur on inselbergs.

As it will be shown later in detail, all these niches, including the bare rock surfaces, are occupied by plant species highly adapted to the specific conditions of the given sub-habitat which form there specific plant communities.

3. Inselberg Habitats

Depending on their size, inselbergs can offer a large variety of different habitats and microhabitats. At an emerging shield inselberg there is only the exposed rock surface as the major habitat with no or only minor differentiation according to exposure. In contrast, at a large inselberg rising up to 100 or more meters, many different expositions occur and habitats may vary from a simple flat rock surface to more complex structures such as seasonal rock pools. As a consequence, the diversity of organisms increases with the number of habitats, and thus, indirectly also with the size of an inselberg.

3.1. Exposed Rock Surfaces

A) Flat rock surfaces, vertical rock surfaces or steep slopes are more or less fully exposed to the sunlight and only periodically shaded (Figure. 4A). They represent the probably most difficult habitat for plant life since no soil cover exists and consequently water availability is the limiting factor. However, if there is rain, this habitat is covered by a closed water film, moistening all organisms at once and disappearing almost as fast as it occurred, depending on inclination and exposure. Water availability is just enough to sustain a lichen cover (film, crust) or an algal film, or both. Only a few species of vascular plants are able to colonize freely exposed bare rock surfaces. In the neotropics, these lithophytes show pronounced systematic affinities to epiphytic relatives.

B) Drainage channels are irrigated by seepage water from vegetation islands (Figure. 4B) or other water reservoirs like rock pools or rock fissures. They are mainly inhabited by algae and lichens.

C) Flush channels are characterized by strong water flow during rain that lasts longer than on other rock surfaces after a rainfall. This however, is enough to provide a different habitat for algae, lichens and vascular plants as well (Figure. 4C)

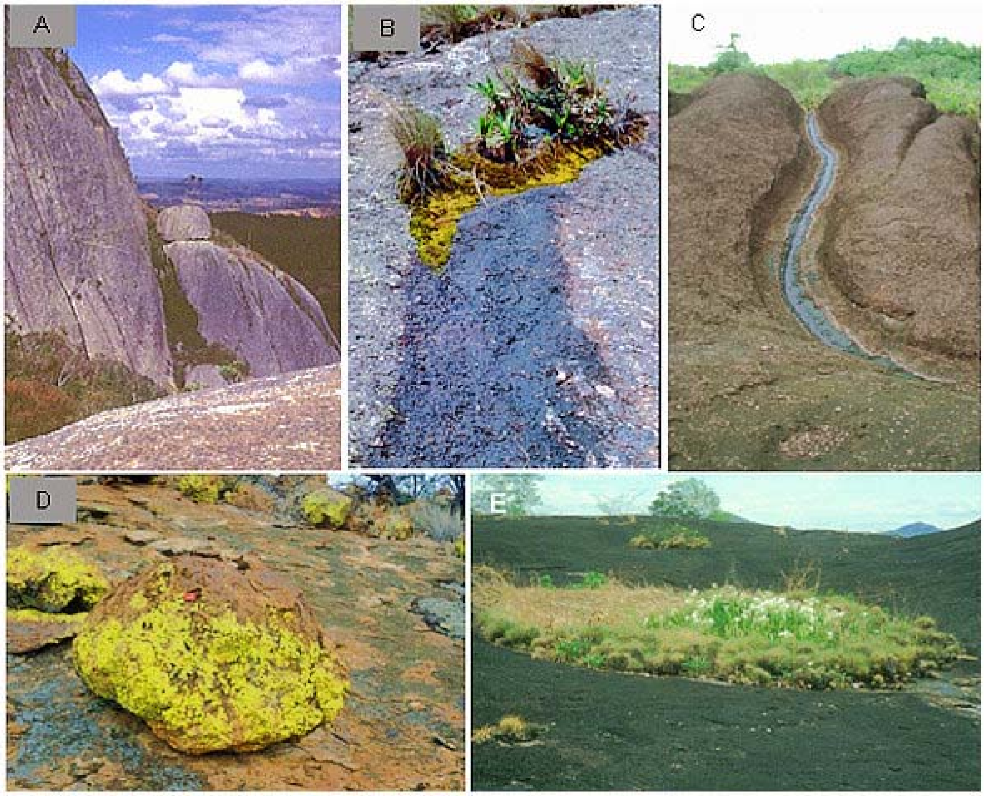

Figure 4 A. Open rock surface at Mt. Angavokely (Central Plateau of Madagascar); B) Seepage site (irrigated by water-flow from vegetation islands on the Pedra Grande–inselberg at Atibaia (State São Paulo, Brazil) [photograph by Ulrich Lüttge]; C. Water tracks (water-flow after rain only) on an inselberg in Venezuela. D: Rock boulders at a Gondwana inselberg. E: Vegetation island with vascular plants, among them flowering *Vellozia* spec. on an inselberg in Venezuela)

D) Rock boulders on the inselberg surface. They receive less water since they are elevated above the covering water film during and after a rain event (Figure. 4D). These boulders can either be without any vegetation in dry savannas or may be covered with a black cyanobacterial film in humid savannas.

3.2. Fissures and Cracks

A) Desquamation fissures (parallel to the rock surface of low volume) are colonized by cyanobacteria or by endolithic lichens (for explanation see section 4.1).

B) Rock fissures (not parallel to the rock surface) are colonized by cyanobacteria only.

C) Rock clefts (up to 2 cm wide, soil development) can host algae, lichens, bryophytes and vascular plants (Figure. 5)

Figure.5 Desquamation fissure on the rock surface on an inselberg in Venezuela. The detritus collected in the fissure provides the substrate allowing *Melocactus mazelianus* to develop roots.

3.3. Rock Depressions

A) Seasonal rock pools are relatively old habitats with an estimated age of several hundred years. Two main types can be distinguished: a) irregularly shaped depressions with a variable depth that can be up to several square meters large; b) round or oval hollows, 10-15 cm deep, covering less than 0.5 m². The latter may also be of human origin created as grinding places (compare section 6). The seasonal rock pools accommodate specialized communities of cyanolichens (for explanation see section 4.1) and highly specialized vascular plants (compare section 5. 2. 2)

B) Rock ponds permanently filled with water offer a relatively constant habitat for algae and vascular plants. However, due to the absence of shallow zones, only vascular plants that preferably grow in wet places can be found occasionally (Figure 6)

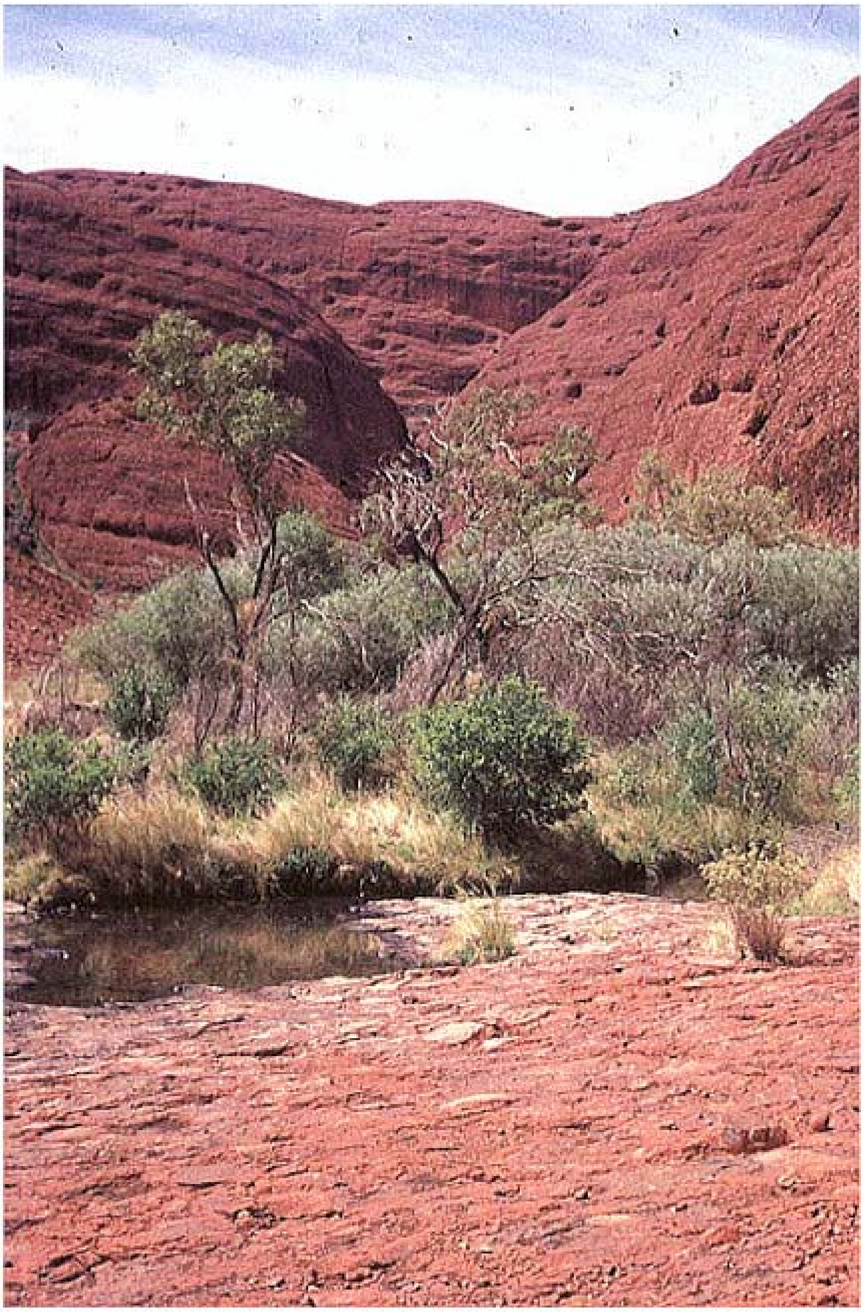

Figure 6. Seasonal water in a rock depression at the Kata Tjuta (Mt.Olgas; Central Australia

C) Depressions with rock debris often are dominated by cryptogams such as cyanobacteria and bryophytes. Among the vascular plants therophytes dominate, but also poikilohydric vascular plants can occur when the soil cover is less than 5 cm deep. Beginning with a soil depth of more than 5 cm vascular plants dominate (Figure. 4E), and on granite inselbergs in South Venezuela it has been shown that increasing soil depth results in an increase of species diversity.

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Biographical Sketches

Manfred Kluge studied at the University of Frankfurt and the Darmstadt University of Technology Biology, Chemistry and Geography. He was graduate student in Botany with Hubert Ziegler at the Faculty of Chemistry, Biology and Geosciences of the Darmstadt University of Technology and received from there in 1964 the degree of a Dr. rer. nat. .After four years as Scientific Assistant at the Institute of Botany in Darmstadt he received in 1969 the Habilitation and worked afterwards as postdoctoral research fellow at the Australian National University, Canberra, in the group of Ralf Slatyer and Barry Osmond. 1970 he became Associate Professor at the Institute of Botany of the Technical University Munich and was called in 1974 as Full Professor of Botany at the Faculty of Biology of Darmstadt University of Technology. Manfred Kluge was Guest Professor at the Botany Department of the National University Singapore and repeatedly Guest Docent of the German Academic Exchange Service (DAAD) at the Botany Department of the University Antananarivo (Madagascar). Several times he was elected Director of the Institute of Botany and the Botanical Gardens of the Darmstadt University of Technology and Dean of the Faculty of Biology of this university. He was chairman of the Research Programm "Biochemical fundaments of ecological adaptation in plants" of the German Research Foundation (DFG), of the DFG Graduate School "Communication in biological systems: From the molecule to the organism in its environment" and Vice Chairman of the DFG Center of Excellence "Molecular Ecophysiology of Plants: Acquisition of resources, membrane transport, regulation of resource consumption". Manfred Kluge was member of the Editorial Boards of several scientific journals, among them "Physiologie Vegetale", "Photosynthesis Research"and "Botanica Acta". Since 2002 he is Professor Emeritus of the Darmstadt University of Technology. His research work is dedicated to the biochemical mechanisms of ecological adaptation in plants, to membrane biophysics and to plant symbioses.

Burkhard Büdel received the diploma in biology from the Philipps-University Marburg, Germany in 1982, the degree of Dr. rer. nat. from the Philipps-University Marburg in 1986 and the Habilitation from the Bayerische Julius-Maximilians-University Würzburg, Germany. He received the honorary membership of the Senckenbergische Naturforschende Gesellschaft, Frankfurt/Main. He has been a faculty member at several universities and, in 1995 he became Professor of Botany at the University of Rostock, Germany, and in 1997 he was offered and accepted the chair of botany at the University of Kaiserslautern, Germany. He was a Heisenberg Fellow of the German Research Foundation (DFG, 1994-1995), the chairman of the German phycologists (1997-2005), a regular member of the expert consultants board of the German Research Foundation for the Antarctic research program (1997-2006), and is an elected consultant of the DFG for ecological plant biology (2000-2008), and of the expert consultant board of the Alexander von Humboldt Foundation for the Georg Forster fellowship program (since 2008). He is in the editorial board of the scientific journals 'Flora' and 'Algological Studies', and the book series 'Fresh Water Flora of Central Europe' and 'Progress in Botany'. B. Büdel was a member of more than 30 scientific expeditions in all continents, including Antarctica. His interests include vegetation, flora, ecology, eco-physiology, systematics and phylogeny of cyanobacteria, algae and lichens of semi-arid and arid ecosystems worldwide and of neotropical rain-forests. He is an expert in the fields of flora, vegetation and ecology of biological soil crusts (BSC) and biofilms on rocks worldwide..